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Effects of available dietary carbohydrate and preslaughter treatment on glycolytic potential, protein degradation, and quality traits of pig muscles[1]

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ABSTRACT: The current study was conducted to determine the interactive effects of a glycogen-reducing diet fed to finishing pigs and length of preslaughter transportion on muscle metabolic traits, proteolysis of intermediate filament and costameric proteins, and meat quality traits. Large White gilts and barrows (n = 48) were selected at 88 kg of BW and individually fed for 21 d a diet (2.6 kg/d) either high (HC) or low (LC) in available carbohydrates. Six gilts and 6 barrows fed the HC and LC diets were subjected to 0 or 3 h of transportation on the day of slaughter. Muscle temperature and pH were measured at 0.5, 1.5, 2.5, 3.5, 4.5, 5.5, and 24 h postmortem in the LM and 24 h postmortem in the dark (STD) and light (STL) portion of the semitendinosus. At 24 h postmortem, glycolytic potential (GP) was determined in the LM, STD, and STL, as well as proteolysis of titin, nebulin, desmin, vinculin, and talin in the LM and STD. The GP was lower ($P < 0.05$) in muscles from LC-pigs than in muscles from HC-pigs. The LC diet also resulted in lower ($P < 0.05$) pH, and a darker ($P = 0.03$), less ($P < 0.01$) yellow color in the STL. The LC diet decreased ($P = 0.04$) cooking losses in the STL and STD. The 3-h journey further decreased ($P = 0.05$) the GP in the STD, regardless of the diet, but transport had no effect ($P \geq 0.67$) on the GP of the LM and STL. Ultimate pH of the LM was lower ($P = 0.02$), and both portions of the semitendinosus were darker ($P = 0.01$) and less yellow ($P < 0.01$), in pigs transported 3 vs. 0 h. In pigs transported for 3 h, intact vinculin tended to be more ($P = 0.08$) degraded in the LM, which coincided with lower ($P = 0.04$) drip losses in the LM of pigs transported for 3 compared with 0 h. Increased ($P < 0.01$) proteolysis of titin paralleled lower ($P = 0.02$) shear force values in the STD of pigs transported 3 vs. 0 h. Although the present results demonstrated the potential of a glycogen-reducing diet to alter the GP of different porcine muscles, the effect of these changes on meat quality traits was limited to higher ultimate pH and darker color in the STL. The positive effects of length of transportation on water-holding capacity (LM and STD) and meat color (STD and STL) were only partially related to the resting muscle glycogen concentration because the 3-h transport lowered the GP only in the muscle with the lowest basal glycogen concentration.

Key words: carbohydrate supply, glycolytic potential, meat quality, pig, protein degradation, transport

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INTRODUCTION

Muscle glycogen concentration at the time of slaughter and the rate of postmortem glycogenolysis and glycolysis regulate lactate accumulation, thereby affecting important meat quality traits (Bendall and Swatland, 1988). Because of different metabolic and contractile properties of the various porcine muscles, antemortem glycogen concentrations differ (Laborde et al., 1985; Bee et al., 2004a), leading to differences in the potential of lactic acid accumulation postmortem and, consequently, to differences in the ultimate pH (Warriss et al., 1989). Besides determining the extent of ultimate pH, muscle glycogen concentration affects the rate of pH decline (Warriss et al., 1989), which could then determine the degree of cytoskeletal and myofibrillar degradation due to calpain-mediated proteolysis (Rowe et al., 2001; Melody et al., 2004).

Results of several studies have shown that muscle glycogen stores in finishing pigs can be decreased at the time of slaughter through strategic feeding of diets low in digestible carbohydrates without compromising growth rate and resulting in positive effects on meat quality (Rosenvold et al., 2001; Bee, 2002). Furthermore, preslaughter conditions such as fasting time before slaughter (Warriss et al., 1989; Wittmann et al.,

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1994) and physical and psychological stress caused by the length of transportation and lairage time (Fernandez et al., 1994; Warriss, 1998; Leheska et al., 2002) also are known to affect glycogen stores.

Therefore, the primary objective of this study was to examine the extent to which glycogen content and quality traits of glycolytic [LM and light portion of the semitendinosus (**STL**)] and oxidative muscles [dark portion of the semitendinosus (**STD**)] could be influenced by a glycogen-reducing diet fed to finishing pigs before 3 h of transportation to slaughter. A secondary objective was to examine the effects of diet and preslaughter transportation on postmortem proteolysis of muscle proteins.

MATERIALS AND METHODS

Animals and Treatments

Swiss Large White gilts and barrows (24 per gender) originating from 6 litters were group-penned and had ad libitum access to a conventional starter diet from weaning to 25 kg of BW. From 25 kg of BW until slaughter, pigs were kept in individual pens (2.56 m^2) on a solid concrete floor in an environmentally controlled building (22°C; 60 to 70% relative humidity). Pigs had ad libitum access to a standard growing-finishing diet until the feeding experiment was initiated when pigs reached 90 kg of BW.

Two isonitrogenous and isocaloric experimental diets were formulated to meet nutrient requirements for finishing pigs weighing 100 kg (Boltshauser et al., 1993). The selected ingredients varied in the amount of highly available carbohydrates and in the amount of fat (Table 1) as previously shown by Lemme et al. (2000). The diet contained a high amount of highly available carbohydrates (**HC**) consisting of wheat starch, wheat, barley, corn, dried sugar beet pulp, sugar beet molasses, dextrose, and soybean meal. The main ingredients of the low available carbohydrate diet (**LC**) were wheat, corn, barley, alkali-treated straw, animal fat, apple pulp, and soybean meal. The diets were pelleted (4.5-mm diameter) at 60°C. During feed processing, feed samples were collected and pooled to determine nutrient content.

At 87.8 ± 1.0 kg of BW, pigs were blocked by litter and gender and assigned from within litter to the 2 diets (2 pigs per gender). Pigs were fed twice daily (0730 and 1600) a total of 2.8 kg (as-fed basis) of the dietary treatments for 21 d, with free access to water. Pigs were weighed weekly and subsequently slaughtered at the research station abattoir (Posieux, Switzerland) 8 d after they reached 100 kg of BW (average BW = 106.9 ± 1.7 kg). The afternoon before slaughter, pigs had access to 1.8 kg of the diet for 1.5 h, after which pigs were deprived of food for at least 19 h.

Pigs were slaughtered on 4 different days to ensure similar BW at slaughter. Six gilts and 6 barrows from both dietary treatments (HC and LC) were subjected to a 3-h (270 km) transport on national roads, and this time span represents the maximum transport time allowed by the 2 major Swiss packing plants. On each slaughter date, the same truck, driver, and loading density (0.67 m^2/pig) were used. At least one gilt and one barrow from each dietary treatment were subjected to the transport. On arrival at the abattoir, pigs were unloaded and allowed to rest for 1 h. The remaining pigs were walked approximately 100 m directly from the pen to the stunning area, avoiding all unnecessary stress, and also rested for 1 h before slaughter. The Swiss Federal Committee for Animal Care and Use approved all procedures involving animals.

Table 1. Composition of the experimental diets, as-fed basis

	Diet[1]	
Item	HC	LC
Barley	16.46	10.00
Wheat	16.60	25.60
Wheat starch	20.00	—
Corn	8.60	18.62
Oats	—	—
Sugar beet molasses	3.00	—
Dextrose	3.00	—
Soybean meal	15.30	17.10
Meat and bone meal	—	—
Potato protein	2.50	1.12
Dried sugar beet pulp	10.20	0.14
Apple pulp	—	5.90
Alkali-treated straw	1.18	11.50
Animal fat	—	7.00
NaCl	0.26	0.02
Dicalcium phosphate	1.56	1.42
Calcium carbonate	0.61	0.80
Lysine-HCl	—	0.05
DL-Methionine	0.01	—
L-Threonine	0.02	0.01
L-Tryptophan	—	—
Pellan[2]	0.30	0.30
Vitamin-mineral-premix[3]	0.40	0.40
Analyzed chemical composition, g/100 g, DM basis		
Crude ash	53	54
CP	166	164
Crude fat	21	104
NFE[4]	713	595
NDF	146	221
ADF	61	113
Calculated nutritional value		
DE, MJ/kg	14.7	14.9
Lysine, g/100 g, DM	0.89	0.90

[1]HC = high amount of highly available carbohydrates; LC = low amount of highly available carbohydrates.
[2]Binder that aids in pellet formation (Mikro-Technik, GmbH & Co. KG, Germany).
[3]Supplied the following nutrients per kilogram of diet: 20,000 IU of vitamin A, 200 IU of vitamin D_3, 39 IU of vitamin E, 2.9 mg of riboflavin, 2.4 mg of vitamin B_6, 0.010 mg of vitamin B_{12}, 0.2 mg of vitamin K_3, 10 mg of pantothenic acid, 1.4 mg of niacin, 0.48 mg of folic acid, 199 g of choline, 0.052 mg of biotin, 52 mg of Fe as Fe sulfate, 0.16 mg of I as $Ca(IO)_3$, 0.15 mg of Se as Na_2Se, 5.5 mg of Cu as $CuSO_4$, 81 mg of Zn as ZnO_2, and 15 mg of Mn as MnO_2.
[4]NFE = nitrogen-free extract (DM – ash – CP – crude fat – CF).

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Slaughtering Procedure and Hot Carcass Sample Collection

A pig was electrically stunned every 10 min using a head-only electric stun tong apparatus (BTR 100 AVS, Freund Maschinenfabrik Gmbh. & Co. KG, Paderborn, Germany). Pigs were subsequently exsanguinated, scalded, mechanically dehaired, eviscerated, and weighed. Thirty minutes after exsanguination, the carcass entered the air-chilling system at 3°C for 24 h. Twenty-five minutes following evisceration, a sample of the LM at the height of the 12th rib was obtained from the right carcass side, immediately wrapped in aluminum foil, placed in liquid N_2, and subsequently stored at –80°C.

Longissimus Muscle pH and Temperature Measurements

The pH and temperature of the LM were monitored 30, 90, 150, 210, 270, and 330 min, as well as 24 h postmortem, using a pH meter (WTW pH196-S, WTW, Weilheim, Germany) equipped with a WTW Eb4 electrode and a temperature probe. The pH meter was calibrated at 30°C for the first 6 pH measurements and at 4°C for pH measured at 24 h postmortem with 2 pH calibration solutions (7.080 ± 0.002 and 4.667 ± 0.006; Wintion, Weilheim, Germany). Sets of measurements were obtained at different locations at the 13th (pH) and 12th ribs (temperature) by insertion of the pH and temperature probes between the ribs from the inside of the left carcass side.

Objective Quality Measures

One day after slaughter, two 1.5-cm-thick LM chops were removed at the 13th rib level from the left side. Furthermore, the semitendinosus was excised, and 2 slices (approximately 70 g) were obtained from the STD and STL portions. From the muscle samples, drip loss and color were determined. Drip loss was measured as the amount of purge resulting during the storage of the chop for 24 h at 2°C (Honikel, 1998). Following a 10-min bloom period, L* (higher value indicates a lighter color), a* (higher value indicates a redder color), and b* (higher value indicates a more yellow color) values for the LM, STD, and STL were measured using a Minolta Chroma Meter (CR-300, Minolta, Dietikon, Switzerland) and illuminant D65. Three replicate measurements were performed on each muscle sample, resulting in 6 measurements per muscle. After drip loss measurements were assessed, muscle samples were vacuum-packaged and stored at –20°C until Warner-Bratzler shear force determination. To assess thawing loss, frozen samples were thawed for 24 h at 2°C. Subsequently, chops and slices were held at room temperature for 1 h, weighed, and then cooked on a preheated (190 to 195°C) grill plate (Beer Grill AG, Zurich, Switzerland) to an internal temperature of 69°C. Chops were weighed after cooking, and the difference between precooked and cooked weights was used to calculate cooking loss percentage. Shear force was determined on the cooked samples cooled to ambient temperature, and eight 1.27-cm-diameter cores were obtained from each LM chop, whereas STD and STL slices were cut into eight strips of 1 × 1 × 5 cm each. Cores and strips were sheared perpendicular to muscle fiber orientation using a Warner-Bratzler shear device (Model 3000, G-R Electric Mfg. Co., Manhattan, KS), and maximum shear force was recorded and averaged across each chop and slice for statistical analysis.

Sample Analyses

Dry matter, ash, CP, crude fat, and crude fiber analyses of feed were carried out according to AOAC methods (AOAC, 1995). The NDF and ADF contents were determined according to the methods of the Verband Deutscher Landwirtschaftlicher Untersuchungs-und Forschungsanstalten (Naumann et al., 1997). Muscle samples were freeze-dried before analysis. From LM samples collected 25 min postmortem, pro- and macroglycogen concentrations were determined as described by Adamo and Graham (1998). The LM, STL, and STD samples collected 24 h postmortem were assayed for glycogen, glucose, glucose-6-phosphate, and lactic acid (Bee, 2002), and glycolytic potential (**GP**; reported in μmol/g of wet tissue) was calculated according to the formula of Monin and Sellier (1985): GP = 2 × [(glycogen) + (glucose) + (glucose-6-phosphate)] + (lactic acid).

Whole-Muscle Sample Preparation and SDS-PAGE Sample Preparation

Samples from the LM and STD (0.5 g) collected at 24 h postmortem were prepared for SDS-PAGE analysis of titin and nebulin and for Western blotting of desmin, vinculin, and talin. Whole-muscle protein extraction and SDS-PAGE gel sample preparation were carried out according to Lonergan et al. (2001). Solubilized protein content of the supernatant fraction was determined following the Lowry et al. (1951) method using premixed reagents (BioRad Laboratories, Hercules, CA). Gel samples were frozen at –80°C until analysis.

SDS-PAGE and Immunoblotting

Gel samples were thawed and run on a 10, 10, and 8% polyacrylamide separating gel [acrylamide:N,N′-bis-methylene acrylamide = 37.5:1 (wt/wt), 0.1% (wt/vol) SDS, 0.5% (vol/vol) N′N′N′N′-tetramethylethylenediamine (**TEMED**), 0.05% (wt/vol) ammonium persulfate (**APS**), and 500 m*M* Tris-HCl, pH 8.8] for determination of desmin, vinculin, and talin, respectively. A 5% polyacrylamide gel [acrylamide:N,N′-bis-methylene acrylamide = 37.5:1 (wt/wt), 0.1% (wt/vol) SDS, 0.125% (vol/vol) TEMED, 0.075% (wt/vol) APS, and 125 m*M* Tris-HCl, pH 6.8] was used for the stacking gel, whereas a 5% polyacrylamide continuous gel [acrylamide:N,N′-bis-methylene acrylamide = 37.5:1 (wt/wt), 0.1% (wt/

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vol) SDS, 0.067% (vol/vol) TEMED, 0.1% (wt/vol) APS, 2 m*M* EDTA, and 200 m*M* Tris-HCl, pH 8.0] was used for determination of titin and nebulin (Melody et al., 2004).

Running Conditions

Gels (10 × 8 cm) for analysis of desmin, vinculin, and talin degradation were run on SE 260 Mini Vertical electrophoresis units (Amersham Biosciences, Switzerland). The running buffer contained 25 m*M* Tris, 192 m*M* glycine, and 0.1% (wt/vol) SDS. Gels were loaded with 20, 80, and 120 μg of total protein/lane for desmin, vinculin, and talin, respectively, and run at a constant voltage of 120 V. Gels (18 × 16 cm) for titin and nebulin were run on a SE 600 Ruby Hoefer unit (Amersham Biosciences). The same running conditions were used as described previously, with the addition of 0.1% (vol/vol) mercaptoethanol. Gels for titin and nebulin analysis were loaded with 80 or 40 μg/lane for the LM and STD, respectively, and run at 10 mA for 24 h. Following electrophoresis, gels for titin and nebulin were stained for one hour with 0.1% (wt/vol) Coomassie brilliant blue R-250, 40% (vol/vol) methanol, and 7% (vol/vol) glacial acetic acid. Gels were destained using an excess of 40% (vol/vol) methanol and 7% (vol/vol) glacial acetic acid. Densitometry scans of the latter gels were performed using the GS-710 densitometer (BioRad Laboratories) and the Quantity One software (BioRad Laboratories). Peak area values of intact titin (approximately 3,000 kDa), nebulin (600 to 900 kDa), and degradation product of titin (approximately 2,400 kDa) in the LM and STR were determined and expressed as a percentage of the respective bands of a reference LM and STR sample (30 min postmortem) loaded on each gel.

Transfer Conditions

Gels for desmin, vinculin, and talin were transferred to polyvinylidene difluoride (PVDF) membranes (Westran Clear Signal; Schleicher and Schuell, Bottmingen, Switzerland) using the TransBlot Cell electrophoresis unit (BioRad Laboratories) at a constant voltage of 90 V for 1.5 h for desmin and vinculin, and at a constant ampere of 1A for 4 h for talin. The transfer buffer consisted of 25 m*M* Tris, 192 m*M* glycine, 2 m*M* EDTA, and 15% methanol (vol/vol) for desmin and vinculin or 10% (vol/vol) methanol for talin. The temperature of the transfer buffer was maintained between 0 and 4°C using a refrigerated circulating propylenglycole (50%, vol/vol) bath.

Immunoblotting

Immunoblotting and chemiluminescent detection were done as described previously by Huff-Lonergan et al. (1996b). Primary antibodies included polyclonal rabbit anti-human desmin (No. V2022, Biomeda, Foster City, CA; diluted 1:20,000), monoclonal mouse anti-human vinculin (clone hVIN-1, Sigma-Aldrich, Saint Louis, MO; diluted 1:10,000), and monoclonal mouse anti-talin (clone 8D4, Sigma-Aldrich; diluted 1:1,000). Secondary antibodies included goat anti-rabbit peroxidase conjugate (No. A 9169; Sigma-Aldrich; diluted 1:20,000 for desmin) and anti-mouse peroxidase conjugate (No. A 2554, Sigma-Aldrich; diluted 1:10,000 for vinculin and talin). Densities of immunoreactive bands were quantified by densitometry using GeneGnome (Syngene, Cambridge, UK) and Gene Tools Analysis Software (Version 3.02, Syngene). Desmin, vinculin, and talin degradation were indicated by a decrease in intensity of the 55, 120, and 225 kDa bands, respectively. Intact protein degradation ratio was calculated as the intensity of the immunoreactive protein band in a LM and STD reference sample (30 min postmortem) that was loaded on each gel.

Statistical Analyses

Data were analyzed as a randomized complete block design with the MIXED procedure of SAS (Version 8.02; SAS Inst., Inc., Cary, NC), with individual pig as the experimental unit. The model used for the ANOVA of growth performance included dietary treatment, gender, and diet × gender interaction as fixed effects, and litter of origin as the random effect. The model used for the analyses of meat quality traits, muscle metabolite concentrations, SDS-PAGE data, and immunoblot data included diet, length of transportation, gender, diet × transportation, diet × gender, transportation × gender, and diet × transportation × gender interactions as fixed effects, litter as the random effect, and date of slaughter as a covariate. The course of the pH and temperature fall of the LM were analyzed as repeated measurements with diet, length of transportation, and sampling time postmortem as fixed effects, date of slaughter as a covariate, and litter as random effect (Littell et al., 1998). The analysis was carried out separately for each gender. Least squares means were calculated, and the PDIFF option of SAS was used to determine differences ($P \leq 0.05$).

RESULTS

Characteristics of Experimental Diets

The HC and LC diets were formulated to be isocaloric and isoproteic (Table 1), although differing in the amount and source of available carbohydrates. This formulation was done primarily by varying the concentrations of crude fat, starch, sugar, and nonstarch polysaccharides. Diet LC contained fewer highly digestible carbohydrates in the form of starch and sugar, but the amount of low-digestible carbohydrates such as cellulose and lignin was 50% greater than in diet HC. To compensate for the lower amount of highly available carbohydrates, 7% animal fat was supplemented to the LC diet.

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Table 2. Effect of diet on growth performance of gilts and barrows

	Diet[1]		Gender			*P*-value[2]		
Item	HC	LC	Gilt	Barrow	SEM	D	G	D × G
ADG, kg	0.92	0.90	0.85	0.98	0.04	0.58	<0.01	0.71
ADFI, kg[3]	2.58	2.56	2.42	2.71	0.06	0.71	<0.01	0.82
G:F[3]	0.36	0.35	0.35	0.36	0.01	0.87	0.23	0.63

[1]HC = high amount of highly available carbohydrates; LC = low amount of highly available carbohydrates.
[2]Probability values for dietary treatment (D) and gender (G) main effects.
[3]As-fed basis.

Growth Performance

Weight gain, feed intake, and G:F were not ($P \geq 0.58$) affected by the diets fed for 21 d (Table 2); however, the offered fixed amount of feed (2.8 kg/d) was not completely ingested because ADFI was, on average, 0.22 and 0.24 kg less than the amount offered in treatments HC and LC, respectively. Regardless of the diets, barrows grew faster ($P < 0.01$) and consumed more ($P < 0.01$) feed than gilts, whereas G:F did not differ ($P = 0.23$) between genders.

Muscle Metabolites

Regardless of the preslaughter transportation, concentrations of glycogen and macroglycogen, but not of proglycogen, were less ($P < 0.05$) 25 min postmortem in the LM of pigs fed diet LC than in the LM of pigs fed diet HC (Figure 1). Feeding diet LC decreased ($P \leq 0.04$) the GP in the LM, STD, and STL compared with diet HC (Table 3). This effect was primarily the result of the lower ($P \leq 0.01$) concentrations of glycolytic intermediates (**GI**) determined 24 h postmortem. Diet LC resulted in lower lactic acid concentrations in the STD ($P = 0.05$), but not in the LM or STL ($P \geq 0.23$). When pigs were subjected to a 3-h journey before slaughter, GP of the STD and lactic acid concentration in the STL were lower ($P \leq 0.05$) than in pigs moved 100 m to slaughter. The GI concentration in the STD of barrows subjected to 3 h of transportation was lower ($P < 0.05$) than in nontransported barrows, whereas no ($P = 0.50$) differences occurred in gilts (gender × transportation, $P < 0.05$). Transportation did not ($P = 0.95$) affect the concentration of glycolytic compounds in the LM.

Protein Degradation

Dietary treatment did not ($P \geq 0.33$) affect intact desmin, vinculin, and talin degradation (Table 4 and Figure 2). In pigs transported 3 h, intact desmin in the STD at 24 h postmortem was less ($P = 0.02$) degraded, and intact vinculin in the LM tended to be less ($P = 0.08$) degraded than in pigs moved 100 m to slaughter. Regardless of diet and preslaughter transportation, proteolysis of intact talin was greater ($P = 0.02$) in gilts than in barrows (26.9 vs. 39.0).

Titin, titin degradation product, and nebulin abundance were not ($P \geq 0.09$) affected by the diet. There were diet × transportation duration interactions on intact titin ($P = 0.02$) and nebulin ($P = 0.08$) degradation. In the LM of pigs fed diet LC and subjected to a 3-h transport, intact titin and nebulin abundance were greater than in the LM of pigs fed diet LC but not transported; however, there was no effect of transportation on titin and nebulin abundance in the LM of pigs fed diet HC (Table 5 and Figure 2). Abundance of titin was lower ($P < 0.01$), and abundance of the titin degradation product was greater ($P < 0.01$) in the STD of pigs subjected to 3 h of transportation compared with pigs moved 100 m to slaughter.

Meat Quality Traits

In barrows, neither pH (Figure 3a) nor temperature (Figure 3c) of the LM measured from 30 to 330 min postmortem was affected by the diet ($P \geq 0.64$) or length of transportation ($P \geq 0.44$). Regardless of the dietary treatment, pH declined more slowly ($P < 0.01$; Figure 3b), and temperature decreased faster ($P = 0.03$; Figure 3d) in the LM of transported gilts than in gilts walked 100 m to slaughter.

The diet affected quality traits of the STD and STL but not ($P \geq 0.31$) of the LM (Table 6). Compared with pigs fed diet HC, STL of pigs fed diet LC was darker (lower L* value; $P = 0.03$), less yellow (lower b* value; $P < 0.01$), with a higher ($P = 0.05$) ultimate (24 h) pH. Cooking losses were lower ($P \leq 0.04$) in the STL and STD of pigs fed diet LC than HC. The diet × gender interaction ($P < 0.05$) indicated that the STL of gilts fed diet LC was less red (lower a* values; $P < 0.05$) than that of barrows (7.4 vs. 9.0), whereas the LM of gilts fed diet LC had a less yellow color (3.4 vs. 4.3; diet × gender interaction, $P < 0.05$) than the LM of gilts fed diet HC.

In the LM of transported pigs, drip loss ($P = 0.04$) and shear force were less ($P = 0.09$), and ultimate pH was greater ($P = 0.02$) than in the LM of nontransported pigs (Table 6). In accordance, the STD from pigs transported 3 h was darker ($P = 0.01$), less yellow ($P < 0.01$), and had less drip loss ($P = 0.03$) and lower shear force values ($P = 0.02$) than the STD from pigs walked 100 m to slaughter. Like the STD, the STL from transported pigs had lower ($P \leq 0.01$) L* and b* values, but greater ($P \leq 0.02$) thaw and cooking losses, than nontransported pigs.

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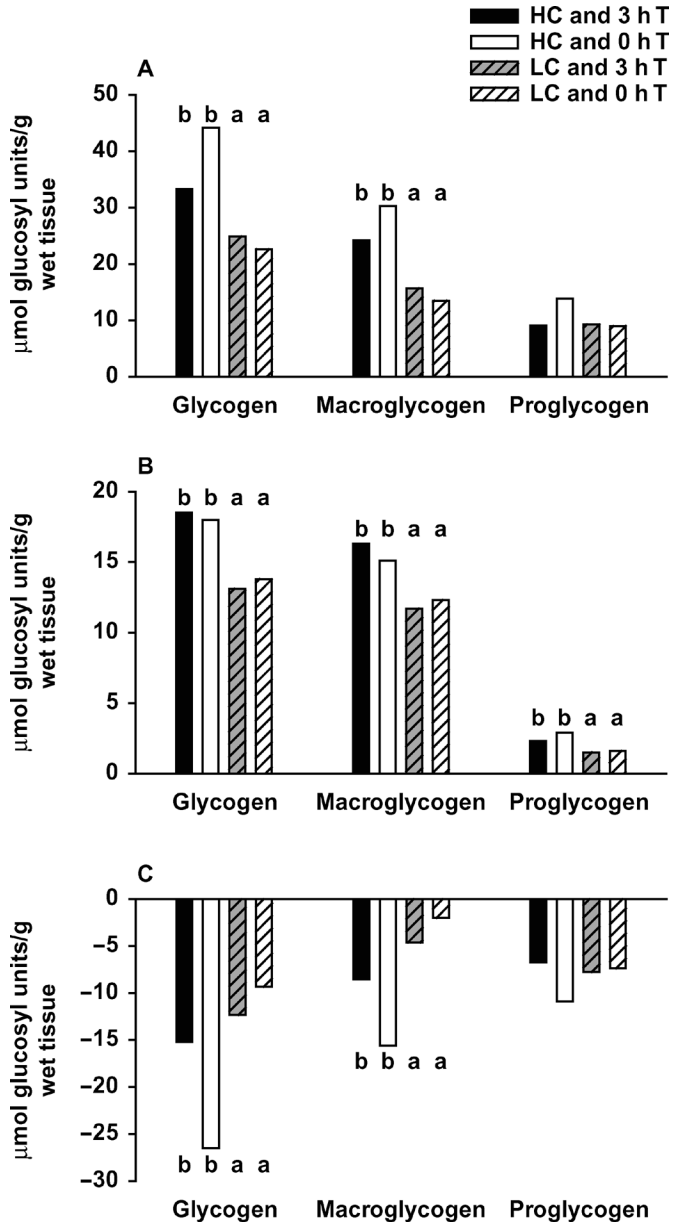

Figure 1. Total glycogen, macro-, and proglycogen concentrations at A) 25 min and B) 24 h postmortem, and C) the decrease in the concentrations from 25 min to 24 h postmortem, in the LM of pigs fed diets with either high (HC) or low (LC) amounts of highly available carbohydrates for 21 d before 0 or 3 h of transportation (T) to slaughter. Bars that do not have common letters differ, $P < 0.05$.

Regardless of the dietary treatment and length of transport, the LM from barrows had greater ($P < 0.05$) L* (51.2 vs. 49.1) and a* (3.1 vs. 2.1) values, as well as lower ($P < 0.05$) shear force values (3.35 vs. 3.64 kg) than the LM from gilts. Similarly, the STD from barrows was lighter (43.5 vs. 40.7; $P < 0.05$) and more tender (3.35 vs. 3.64 kg; $P < 0.05$) than the STD from gilts.

DISCUSSION

Effects of the Diet

In agreement with results obtained in a previous study (Bee, 2002) using similar diets, growth performance was not affected by the diets. The lack of difference between the 2 dietary treatments can be explained by the similar CP and DE concentrations of the diets (Table 1), and the short period of time (21 d) during which the diets were fed. Regardless of the dietary treatments, ADFI was, on average, 230 g less than the offered quantity of feed (2.8 kg/d), and ADFI was particularly low for gilts, which may explain their lower growth rate compared with barrows. Because there were no dietary treatment × gender interactions for either ADFI or ADG, it can be assumed that these differences did not result from the differences in nutrient composition of the 2 diets.

The rate and extent of postmortem glycolysis, combined with the increase in lactic acid concentration, affects the rate and extent of pH decline, thereby determining important meat quality traits. Glycogen is known to exist in 2 distinct pools, pro- and macroglycogen, that can be distinguished based on their solubility in acid (Lomako et al., 1993). The question arises whether the diets used in this study influenced one, or both, glycogen pools and whether postmortem glycogen degradation occurs preferentially in one or both pools. Studies in human skeletal muscle suggest that the pro- and macroglycogen are 2 distinct glycogen pools and that they are subjected to differences in metabolic regulation during exercise (Graham et al., 2001). The proglycogen pool is thought to represent a readily available glycogen source, whereas the macroglycogen pool serves as a reserve (Shearer et al., 2001). Results of the present experiment indicated that glycogen stores were influenced by dietary treatment because macroglycogen concentration 25 min postmortem was less in pigs fed diet LC than diet HC. Furthermore, from 25 min to 24 h postmortem, both glycogen pools diminished, but only macroglycogen was affected by the dietary treatments. Recently, Rosenvold et al. (2003) reported lower macroglycogen accumulation in biopsy samples after feeding a muscle glycogen-reducing diet for 22 d. Compared with antemortem samples, the concentration of proglycogen, but not of macroglycogen, was decreased in the muscle of pigs fed the muscle glycogen-reducing diet at 45 min postmortem (Rosenvold et al., 2003). Besides affecting glycogen pools differently postmortem, a striking difference existed between the 2 studies because the total glycogen concentration was 2 times, whereas proglycogen concentrations were 4 times lower in the current study; however, macroglycogen levels were similar between this study and the one reported by Rosenvold et al. (2003). The fact that the proglycogen pool is the source for readily available glycogen may explain why proglycogen levels were decreased early postmortem in the LM of pigs fed the glycogen-reducing diet

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Table 3. Effects of the diet and the duration of transportation on the glycolytic potential (GP), glycolytic intermediates (GI), and lactic acid concentrations in the LM and semitendinosus (dark and light portions) at 24 h postmortem[1]

	Diet × transport							
	HC		LC			*P*-value[2]		
Item	3 h	0 h	3 h	0 h	SEM	D	T	D × T
LM								
GP,[3] μmol/g of wet tissue	155.3	157.0	148.0	146.9	5.5	0.04	0.94	0.73
GI,[4] μmol/g of wet tissue	24.6	25.2	20.5	20.0	2.5	0.01	0.95	0.76
Lactic acid, μmol/g of wet tissue	106.2	106.5	107.2	106.7	1.8	0.68	0.97	0.78
Dark portion of the semitendinosus								
GP,[3] μmol/g of wet tissue	95.0	106.6	85.3	91.5	5.7	<0.01	0.05	0.54
GI,[4] μmol/g of wet tissue	8.4	13.3	5.8	9.1	1.7	0.01	<0.01	0.53
Lactic acid, μmol/g of wet tissue	78.2	80.1	73.7	73.4	3.3	0.05	0.77	0.69
Light portion of the semitendinosus								
GP,[3] μmol/g of wet tissue	115.5	116.2	106.4	101.5	5.8	0.02	0.67	0.56
GI,[4] μmol/g of wet tissue	9.6	13.6	7.0	7.8	1.9	<0.01	0.09	0.24
Lactic acid, μmol/g of wet tissue	96.1	88.7	92.3	85.3	3.5	0.23	0.02	0.93

[1]HC = high amount of highly available carbohydrates; LC = low amount of highly available carbohydrates.
[2]Probability values for the main effects of dietary treatment (D) and duration of transportation (T), as well as the diet × transportation (D × T) interaction.
[3]GP = 2 × [(glycogen) + (glucose) + (glucose-6-phosphate)] + (lactic acid), Monin and Sellier (1985).
[4]GI = (glycogen) + (glucose) + (glucose-6-phosphate).

(Rosenvold et al., 2003). Our results, combined with the latter observations, suggest that when proglycogen concentration is high glycogen is preferentially catabolized from the proglycogen pool. However, when proglycogen concentration is low, there is glycogenolysis of the macroglycogen pool as well.

To evaluate the effect of the diets on the resting glycogen concentration and the potential of the lactic acid build-up in different muscles, we determined the 24-h postmortem GP (Monin and Sellier, 1985). Regardless of the dietary treatment, concentration of the GI was, on average, 13 μmol/g of wet tissue higher in the LM than in the STD and STL, which indicates that glycogenolysis and glycolysis stopped earlier in the LM than in the semitendinosus, even when GI were still available. One possible explanation was proposed by Kyla-Puhju et al. (2005), who reported that the extent of glycolysis was strongly related to the activity of the glycogen-debranching enzyme. The activity of this enzyme was shown to decrease dramatically at muscle temperature below 35°C and to be practically inactive at 15°C (Kyla-Puhju et al., 2005). In the current study, LM temperature reached 35°C after 60 min postmortem and 15°C after 330 min postmortem; however, ac-

Table 4. Effect of diet and duration of transportation on intact desmin, vinculin, and talin abundance in the LM and dark portion of the semitendinosus at 24 h postmortem[1]

	Diet × transport							
	HC		LC			*P*-value[2]		
Item[3]	3 h	0 h	3 h	0 h	SEM	D	T	D × T
LM								
Desmin	0.85	0.96	0.95	0.87	0.070	0.95	0.81	0.11
Vinculin	0.70	0.99	0.91	0.96	0.114	0.36	0.08	0.21
Talin[4]	0.34	0.32	0.36	0.30	0.053	0.89	0.35	0.62
Dark portion of the semitendinosus								
Desmin	0.95	0.78	0.94	0.87	0.069	0.40	0.02	0.36
Vinculin	1.02	1.09	1.08	1.14	0.090	0.44	0.40	0.98
Talin	0.67	0.64	0.56	0.63	0.087	0.33	0.71	0.41

[1]HC = high amount of highly available carbohydrates; LC = low amount of highly available carbohydrates.
[2]Probability values for the main effects of dietary treatment (D) and duration of transportation (T), as well as the diet × transportation (D × T) interaction.
[3]Ratios were calculated as the intensity of the intact desmin, vinculin, and talin band in each sample over the intensity of the intact desmin, vinculin, and talin band in the internal designated densitometry standard.
[4]Effect of gender, $P < 0.05$.

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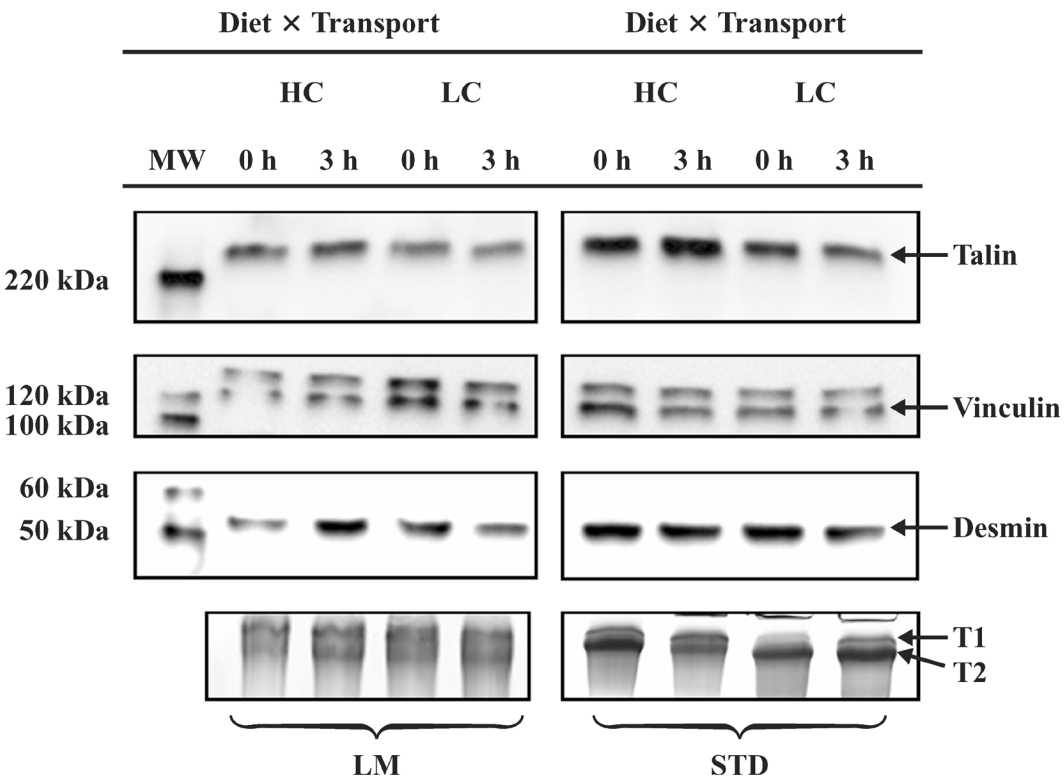

Figure 2. Representative Western blots depicting intact talin, vinculin, and desmin, and a representative coomassie-stained 5% SDS-PAGE gel depicting intact titin (T1) and titin degradation product (T2) at 24 h postmortem from whole muscle extracts of the LM and dark portion of the semitendinosus (STD) from a single pig fed a diet with a high (HC) amount of highly available carbohydrates and a pig fed a diet with a low (LC) amount of highly available carbohydrates for 21 d before 0 or 3 h of transportation to slaughter. The left lane (MW) of each Western blot was loaded with 2.0 μL of MagicMark XP Western Blot protein standards (Invitrogen Life Technologies, Switzerland).

Table 5. Effect of diet and duration of transportation on titin, titin degradation product, and nebulin abundance in the LM and the dark portion of the semitendinosus at 24 h postmortem[1]

	Diet × transport							
	HC		LC			*P*-value[2]		
Item[3]	3 h	0 h	3 h	0 h	SEM	D	T	D × T
LM								
Titin	1.34	1.39	1.79	1.08	0.133	0.88	0.04	0.02
Titin degradation product	2.39	2.07	2.81	2.24	0.127	0.35	0.15	0.75
Nebulin	0.62	0.60	0.96	0.44	0.241	0.76	0.06	0.08
Dark portion of the semitendinosus								
Titin	0.29	0.54	0.28	0.35	0.145	0.09	<0.01	0.20
Titin degradation product	3.55	2.58	3.37	2.87	0.080	0.55	<0.01	0.23
Nebulin[4]	1.15	1.16	1.12	1.10	0.086	0.66	0.99	0.91

[1]HC = high amount of highly available carbohydrates; LC = low amount of highly available carbohydrates.
[2]Probability values for the main effects of dietary treatment (D) and duration of transportation (T), as well as the diet × transportation (D × T) interaction.
[3]Ratios were calculated as the band intensity of titin, titin degradation product, and nebulin in each sample over the band intensity of titin, titin degradation product, and nebulin in the internal designated densitometry standard.
[4]Effect of gender, $P < 0.05$.

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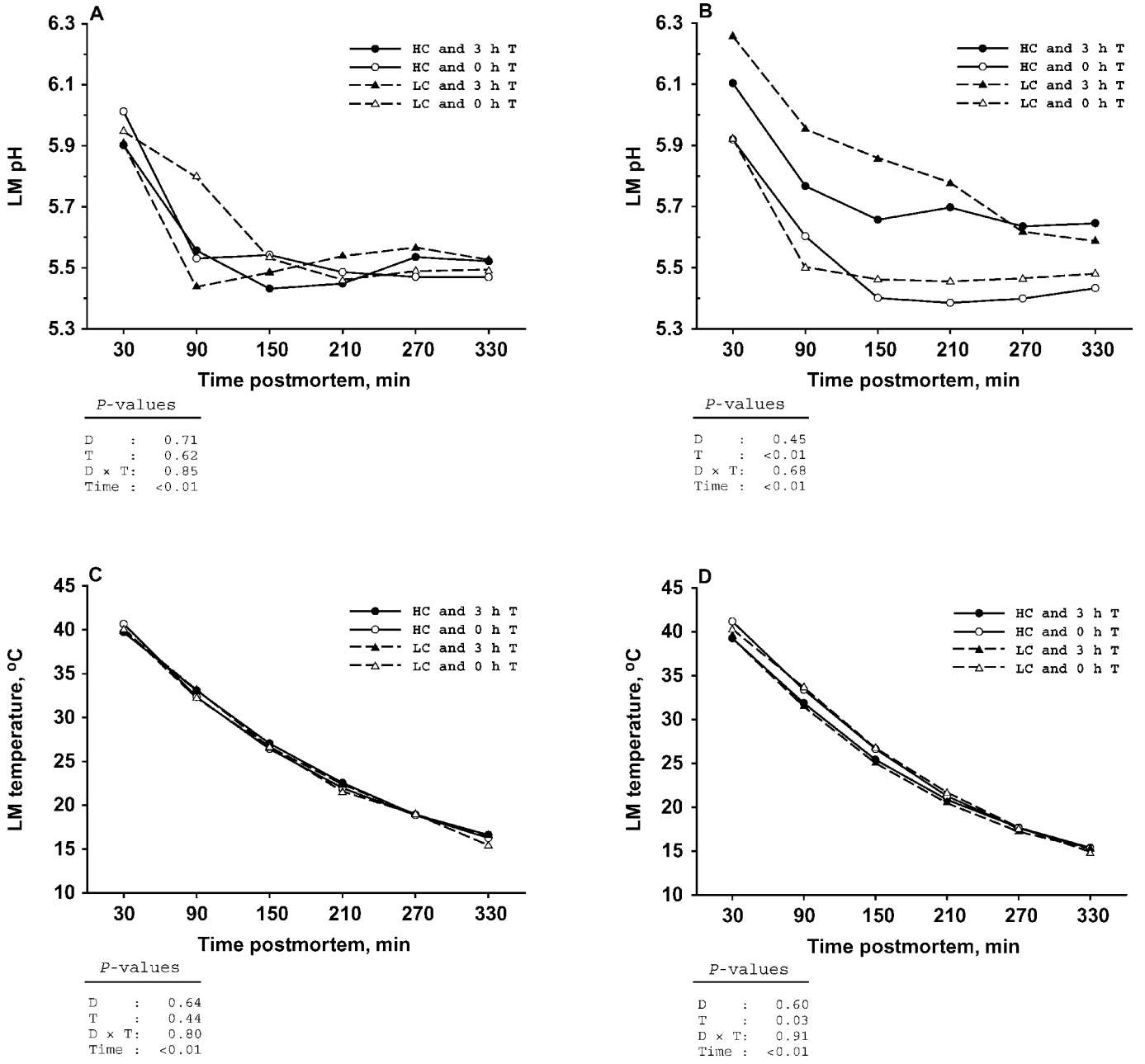

Figure 3. The pH and temperature declines from 30 to 330 min in the LM from barrows (panels A and C) and gilts (panels B and D) fed diets with either a high (HC) or low (LC) amount of highly available carbohydrates for 21 d before 0 or 3 h of transportation to slaughter. Probability values for the main effects of dietary treatment (D), duration of transportation (T), and time postmortem (Time), as well as the diet × transportation (D × T) interaction, are presented for each panel.

cording to Hambrecht et al. (2004), the temperature decline occurs at a much slower rate in hindlimb muscles (semimembranosus). Furthermore, lactic acid concentration was lower (30 and 16 μmol/g of wet tissue, respectively), and ultimate pH was 0.33 and only 0.07 units greater in the STD and STL, respectively, than in the LM. The relatively minor differences in ultimate pH, despite marked differences in lactic acid concentration between the LM and STL, probably resulted from the greater buffering capacity of the LM (Kyla-Puhju et al., 2004).

The extent of the dietary effect seems to be muscle-dependent because the GP of the STD, STL, and LM from pigs fed diet LC was 12, 10, and 5%, respectively, less than from pigs fed diet HC. The observed diet-induced differences could partly result from differences in the muscle fiber composition because greater glycogen concentrations have been reported in fast-twitch glycolytic fibers than in slow-twitch oxidative fibers (Swatland, 1975). Oxidative fibers are up to 6 times more abundant in the STD than in the LM and STL (Bee et al., 2004a), and glycogen depletion occurs faster

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in oxidative than in glycolytic fibers (Wittmann et al., 1994). However, the fiber distribution alone does not account for the greater dietary effect on the GP of the STL compared with the LM. In agreement with previous observations (Christensen et al., 2004; Bee et al., 2004a), the GP was, on average, 42 μmol/g of wet tissue less in the STL than in the LM, despite the similar muscle fiber distribution. The overall lower GP of the STL compared with the LM might be caused by differences in the working load; the LM is primarily involved in posture maintenance and the semitendinosus is implicated in locomotion. Furthermore, the lower basal glycogen concentration in the STL, which was similar to that in the STD, might explain the greater effect of diet LC on antemortem glycogen stores.

Despite the diet-induced decrease in LM GP, initial and ultimate pH, postmortem pH and temperature decline, and meat quality traits were not affected by the dietary treatments, confirming results of previous studies (Rosenvold et al., 2001; Bee, 2002). By contrast, the lower basal glycogen concentration and the lower GP observed in the semitendinosus of pigs fed diet LC resulted in greater ultimate pH and lower L* values in the STL, as well as lower cooking losses in the STD. A possible explanation for the different dietary effects between muscles on quality was proposed by Henckel et al. (2002), who suggested that significant effects on meat quality measurements can only be expected when glycogen concentrations at slaughter were below a certain critical threshold of 53 μmol/g of wet tissue. In agreement with the observations of Bee (2002), results of this study suggest that the combination of low basal glycogen concentrations of the muscle and feeding a glycogen-reducing diet has the potential to produce beneficial effects on pork quality.

Effects of Transportation

The length of transportation primarily affected the concentration of glycolytic compounds and quality traits of the semitendinosus muscle and, to a lesser extent, the quality traits of the LM. The lack of an effect of transportation duration on GP of the LM agrees with results of recent studies by Fernandez et al. (2002) and Leheska et al. (2002). The latter reported no differences in the GP when pigs were transported 30 min or 2.5 h before slaughter, but the GP was markedly decreased in pigs transported for 8 h. One possible explanation for this response was given by Warriss et al. (1998), who showed that a 3-h journey did not induce physical stress when stocking density was adequate (281 kg of live weight/m^2) because pigs could lie down and rest during the journey. By contrast, a very short journey seemed to be more stressful, as evidenced by higher blood lactate and cortisol concentrations at exsanguination in pigs subjected to 15 min of transportation than in pigs transported 3 h (Perez et al., 2002). Guardia et al. (2004) observed that an interaction between length of transport and stocking density on the incidence of PSE was greater when pigs were transported for less than 3 h at low stocking density or during transits longer than 3 h at high stocking density. In the aforementioned studies, the effect of preslaughter treatments were either related with stress indicators in the blood at slaughter or with the concentration of glycolytic compounds and the quality traits of predominantly glycolytic muscles (LM and semimembranosus). Thus, we hypothesized that a more oxidative muscle, like the dark portion of the semitendinosus, could be more prone to differing preslaughter conditions because of the lower basal resting glycogen concentration than predominantly glycolytic muscles like the LM. As anticipated, GP was lower and the concentration of residual GI was greater in the STD of transported pigs than those walked 100 m to slaughter. These differences were reflected in lower L* and b* values, higher water-holding capacity, and improved tenderness of the STD. The lack of a diet × transportation interaction on GP in the STD indicated that the glycogen-reducing effect of diet LC was not accentuated after 3 h of transportation. Even though the GP of the STL did not differ between dietary treatments, GI concentrations tended to be lower, and lactic acid concentrations were greater, in transported than in nontransported pigs, suggesting an effect of transportation duration on postmortem glycolysis. However, differences in the GP of the STD or lactic acid concentrations in the STL obtained in this study seemed to be insufficient to affect ultimate pH, which might also be due to the limited number of pigs included in this study. Furthermore, the present results do not allow the establishment of whether the rate of pH decline was similar and when ultimate pH was reached because the kinetics of enzymes involved in glycogen degradation were not measured. This determinant is important because the combination of low pH and high temperature causes denaturation and decreased solubility of sarcoplasmic and myofibrillar proteins (Sayre et al., 1963; Offer, 1991; Allison et al., 2003), thereby negatively affecting pork color and water-holding capacity (Joo et al., 1999).

In accordance with the lower shear force values, titin degradation 24 h postmortem was greater (lower abundance of intact titin and higher abundance of the titin degradation product) in the STD of pigs subjected to transportation than in pigs walked 100 m to slaughter. The observed relationship between tenderness and titin degradation is consistent with results of previous studies in beef (Taylor et al., 1995; Huff-Lonergan et al., 1996a) and pork (Melody et al., 2004). Contrary to Melody et al. (2004), the greater titin degradation at 24 h postmortem was not paralleled by increased degradation of cytoskeletal proteins. Based on results presented by Kristensen and Purslow (2001) and Bee et al. (2004b), greater degradation of cytoskeletal proteins, like desmin, vinculin, and talin, were expected to be responsible for the improved water-holding capacity in muscle of transported pigs. However, the extent of proteolysis was determined solely at 24 h postmortem, and

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Table 6. Effect of diet and duration of transportation on pork quality traits[1]

	Diet × transport							
	HC		LC			*P*-value[2]		
Item	3 h	0 h	3 h	0 h	SEM	D	T	D × T
LM								
L*[3,4]	51.0	51.2	50.0	50.9	1.10	0.36	0.37	0.63
a*[3]	6.7	6.4	6.2	6.8	0.40	0.86	0.60	0.13
b*[3,4]	2.7	2.7	3.0	2.6	0.49	0.89	0.61	0.60
Drip loss, %	6.62	6.89	5.25	7.90	0.814	0.79	0.04	0.09
Thawing loss, %	6.83	7.48	7.25	6.74	0.632	0.72	0.88	0.21
Cooking loss, %	14.03	13.95	13.13	14.47	0.783	0.75	0.30	0.24
Shear force,[4] kg	3.41	3.54	3.47	3.68	0.122	0.31	0.09	0.69
Ultimate pH	5.57	5.49	5.56	5.48	0.044	0.85	0.02	0.87
Dark portion of the semitendinosus								
L*[3,4]	41.7	43.8	40.0	42.8	1.12	0.16	0.01	0.73
a*[3]	13.6	13.9	13.6	13.9	0.66	0.90	0.45	0.97
b*[3,5]	3.7	4.7	3.6	4.3	0.34	0.22	<0.01	0.43
Drip loss, %	3.66	4.32	2.69	3.92	0.507	0.11	0.03	0.50
Thawing loss, %	7.69	6.90	6.42	7.28	0.619	0.34	0.94	0.08
Cooking loss, %	15.43	16.50	14.06	14.92	0.827	0.04	0.17	0.88
Shear force,[4] kg	4.10	4.48	4.04	4.30	0.152	0.35	0.02	0.68
Ultimate pH	5.87	5.81	5.93	5.82	0.077	0.63	0.18	0.69
Light portion of the semitendinosus								
L*[3,5]	52.9	55.3	49.9	53.4	1.35	0.03	0.01	0.63
a*[3,5]	8.3	8.1	7.8	7.8	0.47	0.19	0.79	0.65
b*[3,7]	3.8	4.7	2.8	3.9	0.32	<0.01	<0.01	0.77
Drip loss, %	4.94	4.74	3.69	4.33	0.606	0.11	0.66	0.40
Thawing loss, %	7.72	6.44	7.27	6.29	0.447	0.42	<0.01	0.69
Cooking loss, %	13.96	13.29	13.30	12.29	0.429	0.02	0.02	0.62
Shear force,[4] kg	4.41	4.11	4.52	4.36	0.256	0.40	0.28	0.73
Ultimate pH	5.54	5.57	5.63	5.65	0.049	0.05	0.48	0.86

[1]HC = high amount of highly available carbohydrates, and LC = low amount of highly available carbohydrates.
[2]Probability values for the main effects of dietary treatment (D) and duration of transportation (T), as well as the diet × transportation (D × T) interaction.
[3]L* = a measure of darkness to lightness (higher L* values indicates a lighter color), a* = a measure of redness (higher a* value indicates a redder color), and b* = a measure of yellowness (higher b* value indicates a more yellow color).
[4]Effect of gender, $P < 0.05$.
[5]Dietary treatment × gender interaction, $P < 0.05$.
[6]Duration of transportation × gender interaction, $P < 0.05$.
[7]Dietary treatment × duration of transportation × gender interaction, $P < 0.05$.

we cannot rule out the possibility that differences in cytoskeletal protein degradation between preslaughter treatments may have occurred later postmortem. It is widely accepted that the extent of pH decline determines the amount of drip loss, and this relationship partly depends on the degree of cytoskeletal and myofibrillar degradation caused by calpain-mediated proteolysis (Ertbjerg et al., 1999; Claeys et al., 2001; Rowe et al., 2001). This mechanism might only be valid when pH values dramatically differ, which was not the case for the STD.

IMPLICATIONS

Applying the appropriate feeding strategy in the finishing period can decrease porcine muscle glycogen concentrations at slaughter without detrimentally affecting growth performance. The dietary effect is greater when the basal muscle glycogen concentrations are low; however, the overall decrease in resting muscle glycogen concentration was insufficient to markedly influence meat quality traits. Improvements in drip loss and pork color were obtained when pigs were transported for 3 h before slaughter, but pork quality improvements were only, in part, the result of the decreased muscle glycogen concentrations and not related to the diet. Thus, severe antemortem glycogen depletion, which could negatively affect pork quality, did not occur in pigs fed glycogen-reducing diets and transported 3 h to slaughter.

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